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THE INHERITANCE OF RESISTANCE TO RUST IN THE SNAPDRAGON[1]

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INTRODUCTION

THE RUST (*Puccinia antirrhini* D. and H.) of the cultivated snapdragon (*Antirrhinum majus* Linn.), was first observed by Blasdale[(2)4] in 1896. For some time thereafter it was apparently confined to the Pacific Coast, but in 1913 it suddenly appeared in the vicinity of Chicago, Illinois, whence it has spread rapidly to all sections of this country, to Mexico, and to Canada. Within recent months it has appeared in England where it will probably become widespread because of the very favorable climatic conditions.

The work of Mains[(4)] indicates that the rust is heteroecious and that it probably has pycnia and aecia on an alternate host. All his attempts to infect snapdragon plants with germinating teliospores were unsuccessful. He predicts that the alternate host will probably be found in California on native species of *Antirrhinum* in localities where those plants are naturally infected with rust.

When the disease first appeared in the Middle West, florists were unable to control or check it, so that the growing of snapdragons under glass became exceedingly hazardous. The rapid spread of the rust was probably caused by the method of propagation then in use. Many florists had their own strains, which they increased by cuttings from a desirable plant. The shade and high moisture conditions of the cutting bench afforded ideal conditions for rust, and interstate shipments of rooted cuttings probably caused its wide distribution.

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[4] Superior figures in parentheses refer to Literature Cited, p. 211.

Peltier[6] demonstrated clearly that the disease is not seed-borne. This fact stimulated propagation by seed, which called for varieties more homozygous for type; and in a short time many were developed, while the cutting method of propagation was discontinued. At present, florists can somewhat control the disease under glass by careful regulation of watering, ventilating, and temperatures.

When snapdragons are grown out-of-doors the disease is almost uncontrollable. Since spraying with fungicides has not given satisfactory results, this flower has almost disappeared from the gardens of many sections.

In California, where practically all the American snapdragon seed is produced, the rust presents a grave problem. Frequently the yields amount to only a few pounds per acre, and 75 pounds per acre is very rare. To increase the yields of seed California seedsmen have followed various practices—notably early planting, and the use of land on which snapdragons have not been previously grown.

An early autumn planting usually produces a large, vigorous plant before the rust becomes active in the spring. Such plants flower early and may have some maturing seed by the time the rust appears. Although this practice is probably beneficial in seasons when climatic conditions do not favor the rapid spread of the disease, the writers have seen several such fields very badly infested in early spring.

When snapdragons are planted, according to the second practice, on soil that has not grown a crop previously, they are usually not very heavily infected. If, however, the same land is replanted year after year, the infestation becomes increasingly severe.

The common practice at present is to withhold water from the plants as soon as rust appears. Though undoubtedly unfavorable for plant growth, this precaution is necessary if the spread of the disease is to be retarded.

METHODS AND MATERIALS

In 1929 the writers became interested in trying to control snapdragon rust by means of resistant varieties. They made trips to some of the large flower-seed ranches in California, observing the disease in every field visited. Since diligent search failed to reveal a single plant showing resistance, there are evidently no "escapes" under conditions of severe infestation.

In 1929 several varieties were grown at Davis, California, and individual plants were self-pollinated to determine whether inbred lines vary in their degree of susceptibility. Dr. J. B. Kendrick, of this Station, also supplied some snapdragon seed of resistant selections, obtained

from Dr. E. B. Mains of Indiana, whose work has been described from time to time in the annual reports of that Station. In 1930 several hundred seedlings were grown from the Indiana seed and from selfed seed produced at Davis. Seedlings of both lots were planted at Colma in the San Francisco Bay region, and on the Waller-Franklin flower-seed

TABLE 1

RESULTS SECURED BY SELFING RESISTANT PLANTS IN 1931; POPULATIONS GROWN IN 1932

Plant No.	Number resistant	Number susceptible	Deviation	$\frac{D}{P.E.}$
4	41	14	0.25	0.11
10	66	0	....	....
12	52	0	....	....
23	106	34	1.00	0.28
24	73	27	2.00	0.68
26	187	64	1.75	0.37
103	68	0	....	....
107	51	0	....	....

TABLE 2

RESULTS SECURED BY CROSSING RESISTANT PLANTS WITH COMMERCIAL VARIÉTIES IN 1931; PROGENIES GROWN IN 1932

Resistant parent and susceptible parent	Number of plants	Number resistant	Number susceptible
10 × Apple Blossom	28	28	0
10 × Salmon Pink	31	31	0
10 × Canary Yellow	14	14	0
12 × Apple Blossom	16	16	0
26 × Canary Yellow	26	16	10
24 × Advance	18	7	11

ranch at Guadalupe, California. A number grown from the Indiana seed showed a very high resistance. Although no plants were completely free from rust, several had only a few small sori. These resistant individuals were allowed to open-pollinate, and a large amount of seed was harvested from each. In 1931 their progenies were grown on the University Farm at Davis, on the Ferry-Morse ranch at Salinas, and on the Waller-Franklin ranch at Guadalupe. In these large populations were found several plants that were entirely free from rust. In the fall a few of the most desirable of the resistant individuals were dug and removed to Davis, where they were transplanted into a greenhouse bench. In 1931 most of them were self-pollinated, but a few crosses were made to the commercial varieties Advance, Apple Blossom, Salmon Pink, Canary Yellow, and Beacon.

The selfed and hybrid seed secured in 1931 was grown in 1932, with the results shown in tables 1 and 2. Not all the data are included in these tables—only sufficient to show that the resistant plants were of two types, one homozygous for resistance and the other heterozygous. The results also indicate that resistance is controlled by a dominant gene.

TABLE 3

RESULTS SECURED IN 1933 FROM SELFING AND FROM CROSSING HOMOZYGOUS AND HETEROZYGOUS RESISTANT PLANTS WITH SUSCEPTIBLE VARIETIES

Pedigree	Number resistant	Number susceptible
Line 26 (heterozygous resistant) × susceptible variety	2,664	2,587
Line 26 (homozygous resistant) × susceptible variety	392	0
Line 10 × susceptible variety	562	0
Susceptible hybrids, self-pollinated	0	310
Heterozygous resistant plants, self-pollinated	363	137
Susceptible hybrids back-crossed to susceptible varieties	0	415

Fig. 1.—A susceptible plant (left) and a resistant plant (right) growing side by side in the field.

In order to check the results further, additional crosses were made by the authors in 1932 between certain resistant plants and some of the more important commercial varieties. Thirty-two resistant plants of line 26 were used as seed parents in crosses with the standard commercial varieties Brilliant Rose, Harmony, Atro-Coccineum, Fascination, Canary Yellow, Snowflake, Cardinal, Apple Blossom, Red Emperor, and Salmon Pink. The resulting progenies were grown in six localities in

California, with the results shown in table 3. The figures given represent the total counts made in the state in 1933.

Of the 32 plants in line 26, 9 proved to be homozygous for resistance. Progeny from all these plants were grown at Davis, Salinas, Guadalupe, Santa Maria, Lompoc, Pasadena, and El Monte. In all locations their reaction toward the rust organism was the same. The results at El Monte were particularly striking; seed was sown in June, 1932, and the plants were wintered-over in the field. In the early spring susceptible plants began to show lesions, and by May they were either dead or badly infected. Figure 1 shows a resistant and a susceptible plant growing side by side in the field.

TABLE 4

BACK-CROSS PROGENIES DESCENDING FROM RESISTANT PLANTS 16 AND 20

	Partially resistant	Susceptible	Resistant
(16 × Salmon Pink) × Salmon Pink	14	29	15
(20 × Beacon) × Beacon	34	61	17

Crosses were also made between plants from the resistant line, No. 10, and the varieties Cheviot Maid Supreme, Apple Blossom, Red Emperor, Beacon, and Advance—all susceptible. All crosses involving plants from line 10 produced only resistant hybrids; all the back-crosses involving a heterozygous plant gave the expected 1 :1 ratio; and those back-crosses and self-pollinations involving susceptible plants gave only susceptible progeny.

MODIFYING FACTORS

Besides the resistant plants two slightly susceptible ones were found in 1931, growing in the progenies of the resistant plants that had been open-pollinated in 1930. These two plants, Nos. 16 and 20, were crossed with commercial varieties, the former to Salmon Pink and the latter to Beacon. From these crosses, only 19 hybrid plants were grown; 10 from the first and 9 from the second. All were planted in the greenhouse. In each lot of hybrids 2 were susceptible, the others being recorded at that time as resistant. In each lot a hybrid which was classified as resistant was back-crossed to its commercial parent in 1932. When these back-cross progenies were examined, three types of plants were found in each population—resistant, slightly susceptible, and susceptible. It is improbable that this situation was the result of the appearance of a second strain of rust, for the three types were found in only two populations, both descending from slightly susceptible plants. These populations

were completely surrounded by other resistant strains, none of which showed this condition.

For this condition no explanation is offered, other than the probable presence of modifying factors. The numbers, though rather small, indicate that an analysis of the situation should not be difficult. It would be very interesting to know whether the factors responsible are carried in commercial varieties. Whenever a plant from line 10 has been used as the resistant parent, it was found to have complete resistance. This statement, however, does not imply that modifying factors are not present in commercial varieties, since only a few of the latter have been used in the crosses.

Fig. 2.—Leaves of snapdragons, showing variations from complete resistance to susceptibility.

Until this situation was encountered the origin of the resistant plants found in populations grown from the open-pollinated slightly susceptible plants of 1930 could not be well explained. If modifying factors are present, segregation might be expected eventually to produce plants from which they had been eliminated. The total population of about 5,000 grown in 1930 presented a wide range from complete susceptibility through different degrees of resistance to complete resistance. Only a few plants were of the latter type. Plants 16 and 20 were selected from among the most highly resistant, so the fact that each produced several resistant plants in the back-cross generations is not unusual, if each carried but few of the modifying genes. Since they had susceptible plants, too, in their progeny, they were also probably heterozygous for resistance. Some of the resistant hybrid progeny of plants 16 and 20 must have carried modifying factors even though they showed no rust in the greenhouse, where conditions for rust are not so ideal as in the field, and where very slightly susceptible plants might easily be counted resistant.

Figure 2 shows the various types of resistance found in the two populations derived from plants 16 and 20, together with leaves from completely susceptible specimens. The snapdragon leaves included in this figure, taken from different plants in line 20, represent fairly well the actual range of resistance. Only a few leaves on such plants are attacked, and often a rather thorough examination is necessary to locate any infection whatever. Other resistant plants are rather heavily infected, but never so severely as fully susceptible ones. The leaves depicted display lesions very similar to those on resistant wheat plants shown by Mains and Jackson,[(5)] whose scale for measuring resistance would be a very interesting method of studying the degrees of resistance in snapdragons. Among the large populations grown in 1931 there were undoubtedly plants showing all types of resistance covered in the scale. In the snapdragon, however, completely resistant plants have not even the light flecking on the leaves, that appears on some wheat plants resistant to leaf rust. This situation is somewhat similar to that reported by Briggs,[(3)] who found evidence for factors modifying the resistance of wheat to bunt, and who gives a rather detailed discussion of modifying factors in general.

METHODS OF ISOLATING RESISTANT PLANTS

In 1932 it was found that susceptible plants could be infected and eliminated in the early stages of growth. According to the procedure used, plants of lines known to carry resistance were transplanted to 2½-inch pots. After becoming established, some were placed in coldframes, the remainder on a greenhouse bench. Every fourth row consisted of various known susceptible varieties. Thus a check was made upon the efficiency of inoculation under both environments. All were then covered with cheesecloth. On several successive evenings each lot was thoroughly syringed with water and had heavily rusted branches shaken over it. The cheesecloth covering was kept moist for several days and then removed; thereafter, the plants were watered and tended normally. The first sori appeared in about ten days, and within three weeks all the commercial plants were infected, as well as the susceptible ones in the selfed and back-cross populations.

DESCRIPTION OF RESISTANT LINES AND OF HYBRIDS BETWEEN THEM AND COMMERCIAL VARIETIES

All four homozygous resistant strains are undesirable as commercial types. The plants are bushy, profusely branching, each producing numerous slender-stemmed spikes. The flowers are small, spaced far apart on the spike, and the colors are generally mottled. The blooming period

being so late, they must be planted from four to six weeks earlier than standard commercial varieties in order to begin blooming at the same time. Each strain is also somewhat self-sterile and does not set much seed even when open-pollinated, although the pollen and eggs are both func-

Fig. 3.—Showing inheritance of rust resistance. Left, Red Emperor, susceptible; right, No. 10, resistant; center, F_1, resistant.

tional. These characteristics would practically eliminate these resistant lines from consideration by florists, gardeners, and seedsmen.

Crosses have now been made between resistant types and 15 standard commercial varieties. In all instances the hybrids resemble the commercial parent more closely than the resistant, as shown in figure 3. They

exhibit marked vigor, are highly self-fertile, bloom almost as early, and have practically as large flowers as does the commercial parent. When a tall variety of the maximum type has been used in the cross, the hybrids are usually as tall as the taller parent. Low-growing, bushy varieties, such as Red Emperor and the Majestics, when crossed with line 10 produce an F_1 population with a growth habit practically the same as that of the commercial parent.

When an F_1 hybrid plant, free from modifying genes, is self-pollinated, it segregates (for rust) into a ratio of 3 resistant to 1 susceptible. If a number of these resistant segregates were self-pollinated, one-third of them would breed true for resistance, and two-thirds, or those heterozygous for resistance, would again segregate in a 3:1 ratio. This work does not purport to analyze the inheritance of any characters other than resistance. Plants in F_2 populations have exhibited a wide range of colors and types.

METHOD OF COMBINING RESISTANCE WITH DESIRABLE CHARACTERS

In order to secure acceptable commercial types as rapidly as possible, the back-cross method has been used. The variety Red Emperor, a low, bushy type with large, dark-red flowers, was crossed with line 10, a type slightly taller in growth, very much branched, and bearing smaller flowers of a mottled rose-and-white color. The hybrid plants were all taller than either parent; their flower color was a dark cerise; they were all resistant to rust and bloomed about a week later than the variety Red Emperor. Several of these hybrids were then back-crossed to Red Emperor, and a 1:1 ratio for resistance was secured. The susceptible plants were discarded, and only the resistant individuals that most closely resembled Red Emperor were selected for use in a second back-cross. This procedure of back-crossing the resistant plants to the commercial parent should be carried through a number of generations until the back-cross population shows a very high uniformity with Red Emperor. Then the best resistant plants should be self-pollinated. The progeny will segregate in a 3:1 ratio for resistance. A large number of the resistant plants should then be self-pollinated, and those homozygous for resistance will form the basis for a new resistant type, which should very closely resemble Red Emperor.

The number of back-crosses necessary to produce a line homozygous for flower color, habit of growth, and general morphological characters will probably vary with different varieties, according to the genetic relationship of the colors and other characters. The inheritance of color in snapdragons is known to be very complex, as shown by Baur[1] and by

Wheldale,[7] who have demonstrated the presence of at least 18 different genes affecting color. Various combinations produce complex color patterns, such as color of the tube differing from the rest of the corolla, and various degrees of mosaic color patterns. In order that a homozygous combination may be secured as rapidly as possible, the commercial parent used in the first cross and in subsequent back-crosses should be as nearly homozygous as possible for color and type. With such a parent, from three to five back-crosses should suffice to produce a fairly homozygous population.

Fig. 4.—Young bud of snapdragon with perianth and two stamens removed.

The procedure described above has been started with the varieties Cheviot Maid Supreme, Autumn Glow, Ceylon Court Yellow, Canary Yellow, Apple Blossom, Red Emperor, Advance, Majestic Red Chief, Majestic Twilight, and Majestic Orange King. First and second back-cross material has already been sent out to California seedsmen. The results so far have been very promising, many resistant plants in the first back-cross generation appearing identical with the commercial parent.

POLLINATION TECHNIQUE

The snapdragon flower is very easy to manipulate for cross-pollination. Emasculation may be performed at any time before dehiscence of the anthers, which does not occur until the buds are large and the flower is

Fig. 5.—Method of bagging for self and cross-pollination.

within a day or two of opening. A young bud at this stage, with the corolla and two stamens removed, appears in figure 4. At this age, when the flower is not readily injured, the stamens may be removed with ease; they are four in number—two long and two short. In the bud stage the filaments are shorter than the style; but they elongate rapidly until, at

dehiscence, the anthers on the longer filaments are in contact with the stigma. The arrangement indicates that self-pollination among snapdragons is common.

When a plant has been selected as a seed parent for a cross, one or more spikes are chosen, and the top of each is pinched out, leaving from 7 to 10 buds. A bag is placed over the spike and fastened to a stake, and a complete record of the cross is placed on a small tag tied below the bag (fig. 5). Emasculation of the buds on each spike may take as long as a week, since the buds progressively mature from the base of the spike to the tip. Pollination is begun as soon as the stigma is receptive—that is, from two to three days after emasculation. Thus both emasculation and pollination may be occurring on a spike at the same time. Pollination is usually accomplished by removing a freshly dehisced anther with a pair of forceps and rubbing the pollen on the stigma. After fertilization, the corolla withers and drops. The seed is harvested as soon as the ovary dehisces, for, if allowed to remain on the plant, it may be partially lost by shattering. The yield will average about 500 seeds per capsule.

RESISTANCE TO RUST IN SOME OF THE OTHER ANTIRRHINUM SPECIES

In 1932 the Division of Foreign Plant Introduction, United States Department of Agriculture, secured seeds of several European species of *Antirrhinum* which were collected by E. Baur (Germany) while on a trip into Spain. In November of 1932, each lot of this seed was planted in the greenhouse at Davis, and in January all were exposed to rust. The seedlings were transplanted to the field in the early spring and were grown in a plot adjacent to susceptible plants of *Antirrhinum majus*. The results of this test appear in table 5.

It is very interesting that resistance to rust should be found in any of the European species. The disease does not occur in Europe, and most likely none of these species have been exposed to this disease at any time during their evolutionary history. Probably, as shown in the table, some were homozygous for resistance, some heterozygous, and others all susceptible. The degree of susceptibility varied considerably, some being attacked very lightly, while others were killed. In all instances the resistance was complete, not a single sorus being found on any of these plants.

Several of the species resembled very closely some of the resistant plants derived from the seed sent by Dr. Mains. The flowers were about the same size, the leaves similar, and the plants also highly self sterile. No attempt has been made by the authors to determine the nature of the

resistance in these plants, but most likely the resistant gene secured from the Indiana material had its origin in some of these European species.

The most generally interesting part of this phase of the work is the demonstration of the great potentialities in the field of foreign plant introduction. Very probably, resistance to many diseases of our economic crop plants could be discovered in closely related forms or species growing in other parts of the world. The desired character, even though

TABLE 5

REACTION OF SEVERAL EUROPEAN SPECIES* OF ANTIRRHINUM TO RUST

Number	Species of *Antirrhinum*	Number of resistant plants	Number of susceptible plants
136	*glutinosum* (Capileira)	32	0
137	*glutinosum* (Orgiva)	0	28
138	*hispanicum* (Celorico)	3	12
139	*ibanjezii* (Cartagena)	16	0
140	*molle* (Lerida)	0	21
141	*molle* (Monsech)	18	0
142	*siculum*	24	0
143	*tortuosum*	0	29
144	species ? (Chorro)	3	8
145	species ? (Cintra)	0	16
146	species ? (Lucena)	10	12
147	species ? (Zaragoza)	17	0

* These species were not determined by the authors, but are here published, with locality names, as listed by E. Baur.

found in another species of the genus, may possibly be incorporated with the more desirable characters of our economic plant. The sanctity of species delimitation is slowly fading as reports of synthetic species formation continue to accumulate.

SUMMARY

The rust (*Puccinia antirrhini* D. and H.), of the cultivated snapdragon (*Antirrhinum majus* Linn.), was first observed in California in 1896. In 1913 the disease appeared in the vicinity of Chicago, Illinois; and since then it has spread to practically all parts of the United States.

Methods of control have not proved entirely satisfactory, particularly when snapdragons are grown out-of-doors. Under greenhouse conditions, the disease can be somewhat checked by certain cultural practices.

In 1929 unsuccessful attempts were made to find resistant plants in the seed fields in California. The next year seed was secured from resistant selections made at the Indiana Experiment Station, and large

populations were grown in several localities in California where rust was particularly severe.

Several plants found in the population from the Indiana seed showed a very high resistance to the disease. These were open-pollinated, and a large amount of seed was harvested from each.

In 1931 progenies from these highly resistant plants were grown in various locations in California, and a very few plants from each location were entirely free from rust. A few of these resistant individuals were removed to Davis, where they were self-pollinated and crossed with several known susceptible varieties. The results showed that resistance is controlled by a single dominant gene.

Several highly resistant plants were used in crosses with known susceptible varieties, and the results indicated the presence of modifying genes. This seems to be a logical explanation for the fact that immune plants were secured from highly resistant parents, since segregation would tend to produce some types free from modifying genes.

The original plants are undesirable types, used only because of their resistance. To transfer the resistant gene to good commercial varieties as rapidly as possible, the back-cross method has been utilized. Progress so far has been very encouraging.

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THRIPS RESISTANCE IN THE ONION

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THRIPS RESISTANCE IN THE ONION[1]

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INTRODUCTION

THE SELECTION and breeding of plants resistant to parasites had its inception chiefly in the field of plant pathology, more specifically in the development of cereals resistant to rust. While the breeding for resistance to insects is still in its infancy, the possibilities in this field appear to be almost unlimited. In certain cases, among which may be mentioned the control of onion thrips, breeding for resistance seems to offer promise. In this paper are presented data which show that in the case of the onion certain varieties do possess a definite resistance to thrips, and the characters thought to be responsible for this resistance are described in some detail.

Howitt,(22)[5] McColloch,(30) Martin,(29) and others have given excellent general reviews of the development of resistant crop plants; here only the more important papers concerned with resistance to sucking insects are reviewed.

The causes of resistance to insects have been grouped by Wardle and Buckle,(43) McColloch,(30) and Wardle(42) as physical, chemical, or physiological. The first category includes such characters as hairiness, thickness of epidermis, thickness of seed coat and rind, and habit of growth; the second, the presence of such compounds as acids, alkaloids, essential oils, and tannin together with the potash-phosphoric acid ratio; the third, such characters as vigor, seasonal adaptation, early maturity, ability to recover from injury, and positive or negative response to specific stimuli. In most instances, however, the characters, whether physical (morphological), chemical, or physiological, are probably genetic in nature and are therefore governed by the laws of inheritance. Resistance may result from one character, or from several combined; and the effectiveness of a character may vary with the soil condition and climate.

Among the physical or morphological characters that seem to be intimately associated with host resistance is hairiness. Hollowell, *et al*,(21) state that the English and Italian types of red clover, which are gla-

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[5] Superior figures in parentheses refer to Literature Cited, p. 230.

brous, suffer much more from the potato leafhopper, *Empoasca fabae* (Harris), than do the American strains, which are hairy. Pieters[34] maintained that the leafhopper was responsible for the development of the hairy American strain. This insect, native to the United States, has probably hindered the reproduction of the more glabrous plants so that only the hairy strains have survived. Fenton and Hartzell[12] thought that the hatching nymphs became entangled in the hairs, whereas Monteith and Hollowell[31] suggested that some character in addition to hairiness may be involved. About the same time Poos[35] found that, in the seedling stages, all varieties of red clover succumbed when injured by this leafhopper; in addition he observed no difference in the amount of injury to Kansas alfalfa and the more hairy Peruvian type. Poos and Smith,[36] and Jewett[23] also concluded that characters other than the amount and type of pubescence are, at least in part, responsible for resistance. Jewett[24] showed that more force is necessary to penetrate the leaf of the Kentucky than other varieties of red clover, a fact which may account in part for its being more resistant than the Italian. A report from South Africa by Worrall[45] stated that the hairy American Upland cotton is more resistant to the jassid, *Chlorita fascialis* Jacobi, than the more glabrous Sea Island and Egyptian varieties. The hairy types are sufficiently resistant to allow the plants to mature the bolls.

At the Kansas Agricultural Experiment Station, 100 species of grasses, comprising about 80 per cent of the native prairie grasses, were tested by Hayes and Johnston[20] for resistance to chinch-bug injury. The native, perennial species with harsh tissues (*Andropogon scoparious* in particular) proved best able to survive injury and recover.

Mumford,[33] discussing the curly-top disease of sugar beets, suggested that the thicker epidermis and cuticle in the resistant strain may indicate some external protection from the beet leafhopper, *Eutettix tenellus* (Baker). In studying the onion thrips on cotton, Wardle and Simpson[44] noted that the underside of the leaves is preferred, apparently because of a difference in epidermal thickness. Bailey[2] observed the same preference on the part of the bean thrips, *Hercothrips fasciatus* (Perg.), on its native hosts.

Staniland[40, 41] found the Northern Spy apple practically resistant to the woolly aphid (*Eriosoma lanigerum* Haus.), but the same degree of resistance did not exist in roots and branches. According to the evidence, the resistance of apple stocks aboveground depends somewhat upon a high per cent of sclerenchyma encircling the stem and preventing penetration. The middle lamella, however, can be dissolved by the saliva of the aphid, so that the check formed by the sclerenchyma may be overcome eventually. He concluded that resistance cannot be ex-

plained wholly by mechanical considerations. *Aphis rumicis* Linn. was found on stocks resistant to woolly aphid. Apparently, then, resistance to these two aphids is associated with different characters. Davidson[8] reported that the saliva of *A. rumicis* can dissolve a passage for the piercing organ but that the presence of a thick cuticle may prevent the *young* aphid from piercing certain tissues. Monzen[32] in Japan thought that a greater pH concentration in the sap or a "specific repellent ingredient" caused resistance of apple stocks to the woolly aphid. Salman[37] considered the Zuccalmaglio-Reinette variety of apple to be resistant to attacks of woolly aphids. Resistance was most noticeable in grafted trees, the stock being infested while the scion was comparatively free. Lepelley,[27] conducting some tests with seedlings derived from crossing the Northern Spy with susceptible varieties, concluded that this variety was heterozygous for resistance.

Even less clearly understood are the chemical factors that are thought in some way to control resistance. Comes[6] stated that acidity of the plant sap caused by organic acids afforded protection and that malic was considered the most toxic. Gernert[15] stated that F_1 hybrids of teosinte and yellow dent corn resembled teosinte and were resistant to attacks of *Anuraphis maidi-radicis* (Forbes) and *Aphis maidis* Fitch. The tougher leaves and more bitter sap of the teosinte parent and the hybrid probably account for their being more resistant than corn.

Andrews[1] showed that a high ratio of potash to phosphoric acid in the tea plant acted inimically to *Helopeltis theivora* Waterh. (a mirid). Though the normal ratio (potash to phosphoric acid) is about 2 to 1, the resistant plants had a ratio of 4 to 1. Attempts to increase the normal ratio gave variable results. Direct injection of potash was not effective. The results of Dementiev[11] on the control of woolly aphid after the injection of barium chloride (1 to 350) into the roots of apple trees were variable. Sanford[38] controlled cottony cushion scale (*Icerya purchasi* Maskell) on Spanish broom by filling with potassium cyanide crystals a hole bored in the trunk.

Although the field of physiological resistance is exceedingly complex, we may well discuss some of the scattered references in the literature.

Harland[16] found that certain native Indian strains of cotton were resistant to leaf-blister mite, *Eriophyes gossypii* Banks. Flint and Hackleman[13] observed that Champion White Pearl, Democrat, and Black Hawk varieties of corn were able to grow vigorously under the same infestation of chinch bugs that killed the more susceptible varieties. Davidson[7] found that the eighteen varieties of *Vicia faba* that he studied were much more susceptible to *Aphis rumicis* than is *V. narbonensis*, the probable prototype of *V. faba*. Resistance seemed to be associated

with the "general physiology of the plant." Searls[39] observed that the degree of aphid infestation (*Illinoia pisi* Kalt.) was less severe on the yellow than on the greener plants or varieties of peas. The same held for alfalfa and sweet clover infested with *Empoasca fabae* Harris.

According to Lees,[26] a mite (no species mentioned) that infests currants and normally feeds on the products of the hypertrophied tissue (the plant's response to the wound stimulus) cannot maintain itself on the red currant *Ribes vulgare,* which develops no hypertrophied tissue. Seabrook's Black, a variety of *Ribes nigrum,* is resistant because the mite kills the growing point and thus starves itself. Harland,[18] reporting that certain varieties of cotton are resistant to the leaf-blister mite (*Eriophyes gossypii* Banks), suggests that resistance results from lack of the gall formation that occurs in susceptible varieties.

In many instances the nature of resistance has not been suggested. Such a case is that of the grape phylloxera, among the first to receive consideration because of its great practical importance. Certain species indigenous to the Mississippi Valley were found to be resistant and have been used successfully as root stocks in infested regions. This subject has been thoroughly discussed by Davidson and Nougaret,[9] Bioletti, *et al,*[4] and Börner.[5]

Beach and Maney[3] secured resistant hybrids by crossing the sand cherry, *Prunus besseyi* Bailey, which is resistant to aphids (no species given), with Montmorency cherry (*Prunus cerasus*) and with Wyant plum (*Prunus americana*), both of which are susceptible. Resistance was found to be inherited as a simple dominant, but its nature was not determined.

Harland[17] observed that two types of Seredo cotton were resistant to the black scale (*Saissetia nigra* Nietn.), but did not suggest the cause of resistance.

Wardle and Buckle[43] stated that the Leconte and Kieffer varieties of *Pyrus,* which are F_1 hybrids between the Chinese pear (*Pyrus sinensis*), resistant to San Jose scale, and the susceptible *Pyrus communis,* resemble *P. sinensis* in resistance.

In none of the cases cited above has the exact nature of resistance been determined. With such a complex condition presenting itself, detailed and highly technical experiments must precede any definite conclusions regarding the exact nature of resistance. Obviously, too, even though the feeding process in the sucking insects mentioned is very similar, the characters causing resistance are not at all comparable, and each problem must be treated individually.

STUDIES ON RESISTANCE TO THRIPS

For three-quarters of a century or more, investigators have sought a satisfactory method of controlling thrips (*Thrips tabaci* Lind) on the onion (*Allium cepa* L.). Although thrips are readily killed by various contact insecticides, usually a number of rather costly applications are necessary. Satisfactory chemical control, indeed, has thus far been impossible for several reasons: A large number of thrips are always protected between the inner leaves of the onion plant, the pupal stage is spent in the soil, the species is very prolific, the generations overlap, natural parasites are lacking, and other host plants are numerous. The enormous damage to the onion crop in California and the unsatisfactoriness of chemical control have necessitated a mode of attack different from that made in the past upon this insect.

Growers who have compared different varieties planted side by side have observed that the Spanish types are somewhat more resistant to thrips injury than are such varieties as Australian Brown and Southport Yellow Globe. The Spanish types do suffer less under conditions of moderate infestation than the so-called American types; but under conditions of extreme infestation as occurred in Davis, California, in 1931 they also were killed prematurely. This difference in the susceptibility of onion varieties suggested the possibility of developing resistant ones, and this work has now been under way for several years at the California Agricultural Experiment Station.

Throughout this investigation, the Division of Foreign Plant Introduction of the United States Department of Agriculture has closely coöperated with the present authors. It has secured seed from many countries, which were tested in the breeding plots at Davis, along with most of the varieties commonly grown in this country. Of chief interest were the introductions from countries of western Asia, especially the area extending from Palestine to India which De Candolle[10] assigned as the probable native home of the onion. In this region, then, we should expect to find the greatest diversity of form, and perhaps a variety with a high degree of resistance.

Comparison of Thrips Population on Different Types of Onions.—In a study of thrips resistance MacLeod[28] in New York State, classified varieties of onions as susceptible, average, and resistant, according to the number of thrips present on the plant. As susceptible, he lists Southport Red Globe, Extra Early Barletta, Red Wethersfield, Mountain Danvers, Ebenezer, and Yellow Globe Danvers; as average, Crystal White Wax, Yellow Strasburg, Prizetaker, and Southport White Globe; as resistant, Utah Valencia, Utah White Sweet Spanish, Valencia, Riverside

Sweet Spanish, Sweet Spanish, Extra Early Red Flat, White Portugal, and Yellow Danvers Flat. The results secured at Davis have not coincided exactly with these. The last three varieties, especially, cannot be classified as resistant here, either as to number of thrips or as to freedom from injury (table 2).

Fig. 1.—The three rows in the foreground to the left are the variety White Persian; the others are Australian Brown. Note the serious damage done by thrips to the latter variety and the freedom of the White Persian from injury. Photographed, June 26, 1931.

In 1931, at Davis, occurred an exceptional opportunity to observe the resistance to thrips of a number of domestic onion varieties and foreign introductions. As conditions were ideal for the rapid increase of thrips, infestation was very severe, and most of the varieties were killed early in the season. The leaves dried from the tips down, causing the premature death of the plants. One introduction, however, FPI 86279 from Persia (fig. 1), remained green throughout the season and showed no injury. This variety, which is here called White Persian, was outstanding in its

resistance. The Spanish types, while showing somewhat less injury than the American, were also killed prematurely.

In 1932 a daily count of the thrips population was made on several varieties (table 1) from May 11 to June 1. In some instances there were only a few plants available for observation. The data, being very interesting, are included here; they agree closely with the results obtained in 1933 (table 2).

In 1933 a more comprehensive test of thrips resistance was made. This included varieties and strains of onions commercially important in the

TABLE 1

VARIETIES OF ONIONS ARRANGED ACCORDING TO THE NUMBER OF THRIPS (ADULTS AND LARVAE) PER PLANT; DAVIS, CALIFORNIA, MAY 11 TO JUNE 1, 1932

Variety	Number of plants	Average number of thrips
White Persian	16	8 0
California Early Red (21-22-1)	38	20.3
Early Grano	4	26.5
Sweet Spanish	68	29.3
Denia	6	31.1
Australian Brown	28	33.2
Italian Red	26	38.3
Yellow Danvers Flat	4	39.2
Red Wethersfield	12	40.0
Southport Red Globe	24	42.0

United States, as well as all the foreign introductions. The seed was sown in the coldframe the last of November. The seedlings were transplanted to the field on March 29 and were spaced 3 inches in rows 27 feet long and 18 inches apart. A plot consisted of ten plants of a strain, and these were replicated five times (except FPI 101113 and FPI 101533). Irrigation water was applied in furrows between the rows. The plants were not treated with insecticides.

In 1933 only the larvae present were counted. These represent rather accurately a definite proportion of the entire thrips population, which is composed of overlapping generations. They cannot fly, are not difficult to count, and remain on the same plant throughout the larval stage.

At each count, the mean number of larvae per plant was determined for each lot of ten plants. These averages were used to determine the frequency distribution.

Counts were begun on May 9 and were repeated at five-day intervals on each strain, until the first plant matured. A plant was considered mature when the top fell. Counts on Nebuka (*Allium fistulosum*) or

Japanese onion were stopped on July 8, although this is a perennial and continues to grow as long as conditions are congenial. The varieties in

TABLE 2

Varieties and Strains of Onions Arranged According to the Average Number of Thrips Larvae per Plant; Davis, California, 1933

Variety	Mean number of larvae per plant	Period of counting, May 9 to date indicated
White Persian	4.14±0.09	July 8
Nebuka (37-1-1)	5.99±0.23	July 8
39-4	6.43±0.16	June 23
FPI 101460; Poona, India	6.68±0.20	June 13
FPI 101499; Poona, India	6.85±0.21	June 13
44-2	6 99±0.20	June 28
Yellow Bermuda	7 00±0.24	June 13
California Early Red (21-22-1)	7.03±0.19	June 23
Australian Brown (5-317-5); light-green foliage	7.06±0.15	July 13
Crystal White Wax	7 23±0.26	June 13
FPI 101461; Poona, India	7.25±0.26	June 13
Italian Red (13-20-3)	7.39±0.16	June 28
Early Grano	7.66±0.18	June 13
Southport White Globe	7.74±0.17	June 18
Prizetaker	7.86±0.18	June 23
Sweet Spanish	8.14±0.16	June 28
White Sweet Spanish	8.16±0.19	June 23
51-3	8.41±0.25	June 28
FPI 101113; Nanking, China	9.08±0.29	June 28
FPI 101112; Nanking, China	9.17±0.24	June 18
FPI 101533; Burma, India	9.28±0.43	June 23
FPI 101575; Pashawar, India	9.38±0.34	June 18
41-8	9.40±0.35	June 18
FPI 101171; Pusa, India	9.41±0.32	June 13
Extra Early Yellow	9.55±0.19	June 18
Australian Brown (commercial)	9.65±0.24	June 23
42-8	9.78±0.24	July 3
White Portugal	9.91±0.31	June 18
Yellow Strasburg	10.02±0.29	June 18
Extra Early Red Flat	10.32±0.28	June 18
FPI 101224; Punjab, India	10.35±0.28	June 23
Australian Brown (5-222)	10.39±0.25	June 23
Mt. Danvers	10.40±0.29	June 18
Yellow Danvers Flat	10.54±0.30	June 23
Red Wethersfield	11.05±0.29	June 23
Ohio Yellow Globe	11.17±0.26	June 23
Ebenezer	11.35±0.25	June 28
Australian Brown (combined pure lines)	11.60±0.25	June 28
Southport Red Globe	11.69±0.26	June 28
Yellow Globe Danvers	12.05±0.26	June 23
Australian Brown (5-16)	12.62±0.31	June 28
Yellow Bottleneck	12.76±0.39	June 28
Australian Brown (5-24)	12.84±0.33	June 23
Southport Yellow Globe	12.90±0.36	June 23

table 2 that bear numbers only, such as 39–4 and 44–2, are selections from foreign introductions that have been selfed for one generation. Of the introductions listed in the table, only White Persian had characters that would make its further propagation desirable.

All varieties were compared with the White Persian, on which the lowest mean number of larvae per plant (4.14) were found. The difference between this number and that of all other varieties and strains is significant. The varieties fall in practically the same order in 1933 (table 2) as in 1932 (table 1), so that certain of their characters evidently in-

Fig. 2.—Nebuka (*Allium fistulosum*) or Japanese onion. The habit of leaf growth in this species helps to restrict the thrips population.

fluenced the size of the thrips population. The Nebuka, figure 2, which has foliage somewhat like that of White Persian has a thrips population nearly as low, but its leaf tissue is much more severely injured where the thrips have fed.

Most of the Australian Brown strains are severely injured by thrips and, as shown by table 2, support a large population. There is, however, one exception—namely, Australian Brown 5–317–5, which has been inbred for two generations and has foliage similar in color to that of Sweet Spanish.

Nature of Resistance in the White Persian.—The resistance of the White Persian to thrips seems to be determined by two groups of factors: one, probably, controls those characters that hold the thrips population to a minimum; the other helps the plant to withstand injury. Two, or perhaps three, characters apparently tend to restrict the thrips population—namely, the shape of the leaves, the angle of divergence of the two innermost leaves, and the distance apart of the leaf blades on the sheath column. Probably of considerable importance is the difference in shape of the leaves. In most varieties the leaf blades have a flat side; these sides are face to face and, in the young leaves, closely appressed, protecting the larvae against insect enemies and adverse weather conditions. In White Persian the leaves are almost circular in cross section (fig. 3), reducing protection to a minimum.

Fig. 3.—Australian Brown on the left; White Persian on the right. Note the habit of growth.

The leaf blades of ten White Persian plants were pulled together and tied in order to increase the amount of contiguous leaf surface and thus determine whether the greater protective area formed would cause an

increase in the thrips population. Ten plants of the Denia variety were handled in the same manner. Ten other plants of each variety not tied, were used as checks. Before tying and at about seven-day intervals thereafter, the number of larvae per plant was determined. The counts are presented in table 3.

The marked increase in the number of thrips on the plants whose tops were tied shows that closely bunched leaves make a very favorable environment for this insect. This also indicates that resistance in the White Persian is probably not caused by some toxic component within the plant, since the percentage increase in the number of larvae per plant

TABLE 3

Mean Number of Larvae per Plant with Foliage Tied and Untied; 1932

	Number of thrips on date tied, July 14	Number of thrips after		
		8 days	15 days	21 days
Denia, leaf blades tied	78.7	139.3	122.8	37.4
Denia, leaf blades not tied (check)	115.0	81.5	44.8	16.8
White Persian, leaf blades tied	19.3	60.5	80.4	20.3
White Persian, leaf blades not tied (check)	26.1	25.7	3.6	0.9

after the leaves were tied was more rapid in White Persian than in Denia. The later downward trend of the population was caused by the maturing of the plants.

The wide angle between the two innermost emerged leaves (fig. 3), especially in the young plant, is another White Persian character that helps to restrict the thrips population by reducing the protective environment to a minimum. Still another character, probably of some importance, is the greater vertical distance between the leaf blades. Each new leaf extends its sheath farther beyond the one encircling it than in other commonly cultivated varieties (fig. 3). This habit of growth produces an extremely long sheath column. If commercial varieties of onions had these leaf characters, one might secure a more efficient control by spraying or dusting than at present, because practically all of the foliage could be covered.

As stated above, the shape and habit of leaf growth in the White Persian probably help to restrict the number of thrips. Other characters help the plants to withstand injury, but these are as yet not well understood.

As has often been observed, thrips injury becomes most conspicuous following the first hot days of summer when there is a desiccation and dying back of the foliage; but it is not known just how high temperatures

accentuate thrips injury. This typical injury is most prominent in varieties with dark-green foliage; less so in the Spanish types which have lighter-green foliage, and is apparently absent in White Persian which has foliage that is even lighter green than that of the Spanish types. Leaf color may be a factor in resistance to injury, because the temperature in the White Persian leaf tissues is possibly lower than in those varieties having darker-green foliage. Similarly, in the tomato fruit, Harvey[19] found dark-green areas to be more subject to injury by sunscald than light-green areas, because of the greater absorption of light with a consequent higher temperature in these areas.

In the White Persian one can determine the exact location where the thrips have fed because these areas are somewhat lighter green in color than the surrounding tissue but they do not seem to dry out. As a thicker leaf tissue might conceivably help to prevent desiccation of the cells surrounding the injured areas, measurements were made to find whether there was a difference between leaves of varieties showing different degrees of resistance. The varieties used were White Persian, Sweet Spanish, and Australian Brown. Sections were taken of the entire circumference at the widest part of mature leaf blades. These were killed, sectioned, stained, and made into permanent slides in the usual manner. The image of the section was projected with a Zeiss microprojector upon a screen, and at each bundle the thickness of the tissue was measured. Leaves of about fifty plants of each variety were so studied. If the thickness of the Australian Brown is taken as 1, then the Sweet Spanish has a value of 1.13; the White Persian 1.32. Analyzed statistically, the differences between the mean thickness of the Australian Brown and White Persian, and Sweet Spanish and White Persian were found to be significant. The difference between Australian Brown and Sweet Spanish may, however, be unimportant. Leaf thickness alone probably does not account for resistance to injury, because certain White Persian plants had leaves about the thickness of Australian Brown but still without typical injury.

History of the White Persian.—The White Persian variety of onion was obtained by Dr. W. E. Whitehouse of the United States Department of Agriculture, Division of Foreign Plant Introduction, in 1929, while he and H. L. Westover were traveling through Europe and Asia Minor to study and collect the forage, fruit, and vegetable crops indigenous to that part of the world. A number of varieties of onions were secured in Persia; but there, according to Dr. Whitehouse, the peasants considered the best onion to be a large white one grown under irrigation in Kashan, a village situated in the hills about 3,000 feet above sea level. Seed of this variety was distributed from Washington as FPI 86279. It was

later named White Persian by the California Agricultural Experiment Station.

Characteristics of the White Persian.—Three crops of White Persian bulbs and two crops of the seed have now been grown at Davis. Although selections have been made within the variety for certain leaf characters, very little attention has been given to the isolation of desirable bulbs. Probably the best use of this variety at present is to cross it with the existing important commercial types, thus incorporating in them the resistant characters.

The chief objections to the variety as a commercial onion are its tendency to split badly and its poor keeping quality. Its strong tendency to bolt is no worse than that of some other varieties. When seeded in coldframes on September 4, 1931, and transplanted to the field on December 17, about 98 per cent of the plants bolted the following spring. Very little bolting occurred when seeding was done in the coldframe in late November and the transplanting was done in March.

As stated previously, the foliage is of a lighter green than that of any other variety ever grown in the plots at Davis. The innermost leaf, as it emerges, bends away somewhat from the next oldest leaf; and the sheath of the new leaf extends considerably beyond the one encircling it, causing the mature onion to have a conspicuously long sheath column. The leaf blades of the young plant are round in cross section, but those that arise later are more flattened.

The plants mature very late. The bulbs are white and oblate. The flavor is exceptionally mild—probably milder than that of any of the commercial varieties now grown in this country—and unlike that of any other onion variety known to us.

Breeding for Resistance.—An effort is now being made to incorporate the resistance characters of White Persian into susceptible varieties. At present, F_2 and first back-cross generations are being grown in the field and in the greenhouse. In order to expedite the work, the plants are being handled so that one generation is grown each year. If the seed is sown in July, the plants have a longer growing season, and most of them go to seed the following spring.

The first crosses between White Persian and other varieties were made by intermingling under muslin cages. Flies were introduced to do the pollinating, as described elsewhere (Jones and Emsweller[(25)]). Seed from these White Persian parents was sown in the coldframe; and the F_1 plants having a darker foliage color could be selected from among the seedlings. Some of them were selfed; others were back-crossed to commercial types. Selfing was accomplished by enclosing each umbel within a one-pound manila paper bag; back-crossing, by emasculating

an infloresecence of the plant to be used as the female parent, tying to it one from the pollen parent, and enclosing both within a small cheesecloth cage. In some cases the plants that were to be crossed were grown side by side (fig. 4). In other cases the flower stem of the pollen parent was severed near the base and placed in a bottle of water, where it re-

Fig. 4.—The two small cages in the foreground are made of a wire framework and covered with cheesecloth. Flower heads of the male and female parents are enclosed within, and flies are added to carry on pollination.

mained fresh and produced pollen for more than a week. Flies, hatched artificially, were placed within the small cages enclosing the two umbels; and a set of from 700 to 800 hybrid seeds was often secured. Crossing by means of flies is much more efficient than crossing by hand.

As stated previously, the bulbs are very poor keepers; as a rule they rot and sprout soon after being placed in storage. If set in the field, they usually make a good growth until about the time the plants start to

bloom, but often die from various bulb rots before much of the seed is mature. Fair results have been secured by disinfecting the bulbs shortly after they have been harvested and then planting them in sterile soil before they begin to sprout. This method is used only for plants that are needed for breeding. For the production of large quantities of seed, the plants are not permitted to bulb. If seeding is done in July or in early August, the plants become large and are then set in the field some time during the winter. At Davis these plants produce a good yield of seed and remain in a healthy condition until practically all the seed is mature.

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